

# Hardwood riparian forests in northern Iberian Peninsula: classification and diversity patterns

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Academic editor: Jozef Šibík ♦ Linguistic editor: Megan McNellie

Received 26 December 2024 ♦ Accepted 20 March 2025 ♦ Published 27 May 2025

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## Abstract

**Aims:** Temperate hardwood riparian forests constitute an endangered habitat occurring mostly on the floodplains of major European rivers, and included in habitat T13 of the European Nature Information System (EUNIS). In this study we aim to 1) confirm their presence in small rivers of northern Spain, 2) revise their classification at association level, and discuss it at alliance level, 3) evaluate their diversity patterns and ecological preferences. **Study area:** Inner temperate and submediterranean valleys in northern Spain. **Methods:** We sampled 72 nested series of vegetation plots with grain sizes ranging from 0.0001 m<sup>2</sup> to 200 m<sup>2</sup>, where the presence of vascular plants was recorded in all grain sizes and their cover estimated in 100 m<sup>2</sup>. 200 m<sup>2</sup> plots were submitted to the EUNIS Expert System (EUNIS-ESy) and to agglomerative hierarchical clustering. Non-metric dimensional scaling was used for their ordination in the multivariate space. Diagnostic species were assessed by means of modified phi index and differences among forest types regarding their diversity and ecological preferences through analyses of variance. **Results:** The EUNIS-ESy classified five plots in habitat T13, 19 were classified in other deciduous forest types, and 48 were classified only at level 1 (forests) or remained unclassified. Three main clusters emerging from the agglomerative clustering corresponded to three associations from the alliance *Alnion incanae*: *Carici pendulae-Fraxinetum excelsioris*, *Galio laevigati-Fraxinetum excelsioris*, and *Viburno lantanae-Ulmetum minoris*. The mean species richness per plot was 75.3, with the highest values in the western Pyrenean association *Galio-Fraxinetum*, while Shannon diversity was lowest in the submediterranean *Viburno-Ulmetum*. **Conclusions:** These riparian forests provide refuge for several endangered species and might mark the southwestern distribution of hardwood riparian forests in Europe. It is therefore crucial to clarify their classification at alliance level, for which a comprehensive analysis of European temperate riparian, alluvial and mesic oak forests is required.

**Taxonomic reference:** Euro+Med PlantBase (Euro+Med 2024).

**Syntaxonomic reference:** Mucina et al. (2016), updated in Chytrý et al. (2024), for high rank syntaxa; Biurrun et al. (2016) for associations and suballiances.

**Abbreviations:** CWM = Community Weighted Means; DIV = Disturbance Indicator Values for European plants; EDGG = Eurasian Dry Grassland Group; EIVE = Ecological Indicator Values for Europe; EUNIS = European Nature Information System; EUNIS-ESy = EUNIS Expert System; NMDS = Non-Metric Multidimensional Scaling; SAR = Species Area Relationship.

## Keywords

*Alnion incanae*, alpha diversity, beta diversity, *Fraxino-Quercion roboris*, hardwood riparian forest, Iberian Peninsula, nested-plot, northern Spain, species-area relationship, syntaxonomy, *z* value

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## Introduction

European temperate hardwood riparian forests are one of the richest woodland types in Europe, with a diverse and structurally complex understory. They are typical of less-frequently flooded, well-aerated mineral soils on floodplains of the middle and lower reaches of major European rivers (Chytrý et al. 2020). The forest canopy is usually tall and multi-layered and combines several tree species, like ashes (*Fraxinus excelsior*, *F. angustifolia*), alder (*Alnus glutinosa*, *A. incana*), and elms (*Ulmus glabra*, *U. minor*, *U. laevis*), among others (Rodwell and Ssymank 2016). The forest understory includes small trees, shrubs and lianas, as well as a diverse herb layer with an admixture of vernal geophytes and hemicryptophytes. Many of these herbs also occur in mesic oak forests, while some, especially hemicryptophytes, are indicators of wet or moist soils.

These forests, included in the habitat T13 of the European Nature Information System (EUNIS; Chytrý et al. 2020), are categorized as Endangered habitat in the European Red List of Habitats (Janssen et al. 2016). Although Spain was not considered in the evaluation of this habitat, this is, in fact, included in the Spanish list of terrestrial habitats (MITECO 2024). Additionally, maps generated by the EUNIS Expert System (EUNIS-ESy) and provided by Chytrý et al. (2020) assign to habitat T13 many plots from northern Spain, mostly from the Pyrenees and adjacent temperate and submediterranean areas in the Basque Country and Catalonia. Therefore, even though there are no large rivers and floodplains in the temperate part of northern Iberian Peninsula, the presence of this habitat in Spain should be further investigated, as until now the vegetation plots mapped in Chytrý et al. (2020) are the only evidence about it. Actually, the fact sheet corresponding to this habitat produced during the evaluation of the European habitats (Janssen et al. 2016) indicates that although it is especially characteristic of the middle and lower reaches of major European rivers it also occurs throughout Europe as smaller stands in younger river valleys (Rodwell and Ssymank 2016).

Habitat T13 partly overlaps with the alliances *Alnion incanae* and *Alno-Quercion roboris* and it completely includes the alliance *Fraxino-Quercion roboris* (Chytrý et al. 2020). The alliance *Alnion incanae* has been traditionally recognized to be present in northern Spain (Rivas-Martínez 2011), but *Alno-Quercion roboris* and *Fraxino-Quercion* have never been documented (but see Mercadal and Vilar 2013), and are not indicated for Spain in the recent maps of European phytosociological alliances (Preislerová et al. 2022). The lack of documentation of the presence of *Fraxino-Quercion* and *Alno-Quercion roboris* in Spain also applies to the suballiance name *Ulmenion* Oberd. 1953, traditionally used to include the syntaxonomic content of *Fraxino-Quercion* and considered as part of the *Alnion incanae* (Mucina et al. 2016). The suballiance *Ulmenion* separates the elm and ash dominated riparian forests growing on the river floodplains only subject to episodic floodings, mostly in lowlands, from the alder dominated forests growing on the river edge, more frequent in mountains and hills (Wallnöfer et al. 1993). In

Spain, the alliance *Alnion incanae* is found in the Pyrenean valleys and surrounding temperate and submediterranean areas, mostly in Catalonia and Navarre. It also occurs in the Atlantic region, although restricted to the inner subcantabrian valleys, i.e., the upper sections of the big Mediterranean rivers Duero and Ebro and their tributaries in the southern watershed of the Cantabrian Range and Basque-Cantabrian mountains (Biurrun et al. 2016). In the Cantabrian valleys, formed by the streams flowing to the Bay of Biscay, the *Alnion incanae* is replaced by the alliance *Hyperico androsaemi-Alnion glutinosae* (Biurrun et al. 2016).

The spatial co-occurrence of the habitat T13 (Chytrý et al. 2020) and the alliance *Alnion incanae* (Biurrun et al. 2016) in the Pyrenees and inner valleys of the Atlantic region suggests that northern Iberian hardwood riparian forests correspond, at least, to some of the six associations that Biurrun et al. (2016) included in this alliance, for which they described the new suballiance *Buxo semperfurentis-Alnenion glutinosae*. This suballiance gathers Pyrenean and Iberian alder and ash forests growing in mountain streams on calcareous substrata, under temperate eucceanic sometimes submediterranean climate. The six associations are distributed in the southern foothills of the Cantabrian Range (*Euphorbio hybernae-Fraxinetum excelsioris*), the subcantabrian (*Carici pendulae-Fraxinetum excelsioris*) and submediterranean (*Viburno lantanae-Ulmetum minoris*) valleys of the Basque Country and Navarre (Basque-Cantabrian mountains), the western Pyrenean valleys (*Galio laevigati-Fraxinetum excelsioris*), the Prepyrenean valleys in Aragón (*Lathraeo clandestinae-Populetum nigrae*) and the Central and Eastern Pyrenean valleys (*Equiseto hyemalis-Alnetum glutinosae*).

In this work, we focus on the riparian forests of the inner Basque-Cantabrian and western Pyrenean valleys to assess their current phytosociological classification and confirm their correspondence with EUNIS habitat T13, as well as to obtain further knowledge on their diversity patterns and ecology. With this aim, we sampled 72 new vegetation plots in the same or nearby locations to many plots already used by Biurrun et al. (2016), following a standardized sampling design. Specifically, our aims were 1) to apply the EUNIS-ESy to these new vegetation plots in order to obtain their habitat level classification and eventually confirm their correspondence with habitat T13; 2) to check if the phytosociological classification at association level emerging from a vegetation classification attempt at the scale of the Iberian Peninsula replicates at a regional scale; 3) to compare the diversity patterns and structural and ecologic features of the different hardwood riparian forests occurring in the region.

## Study area

The study area includes the inner (subcantabrian and submediterranean) valleys in the Basque-Cantabrian mountains, as well as the westernmost Pyrenean valleys, belonging to the autonomous regions of Basque Country and Navarre.

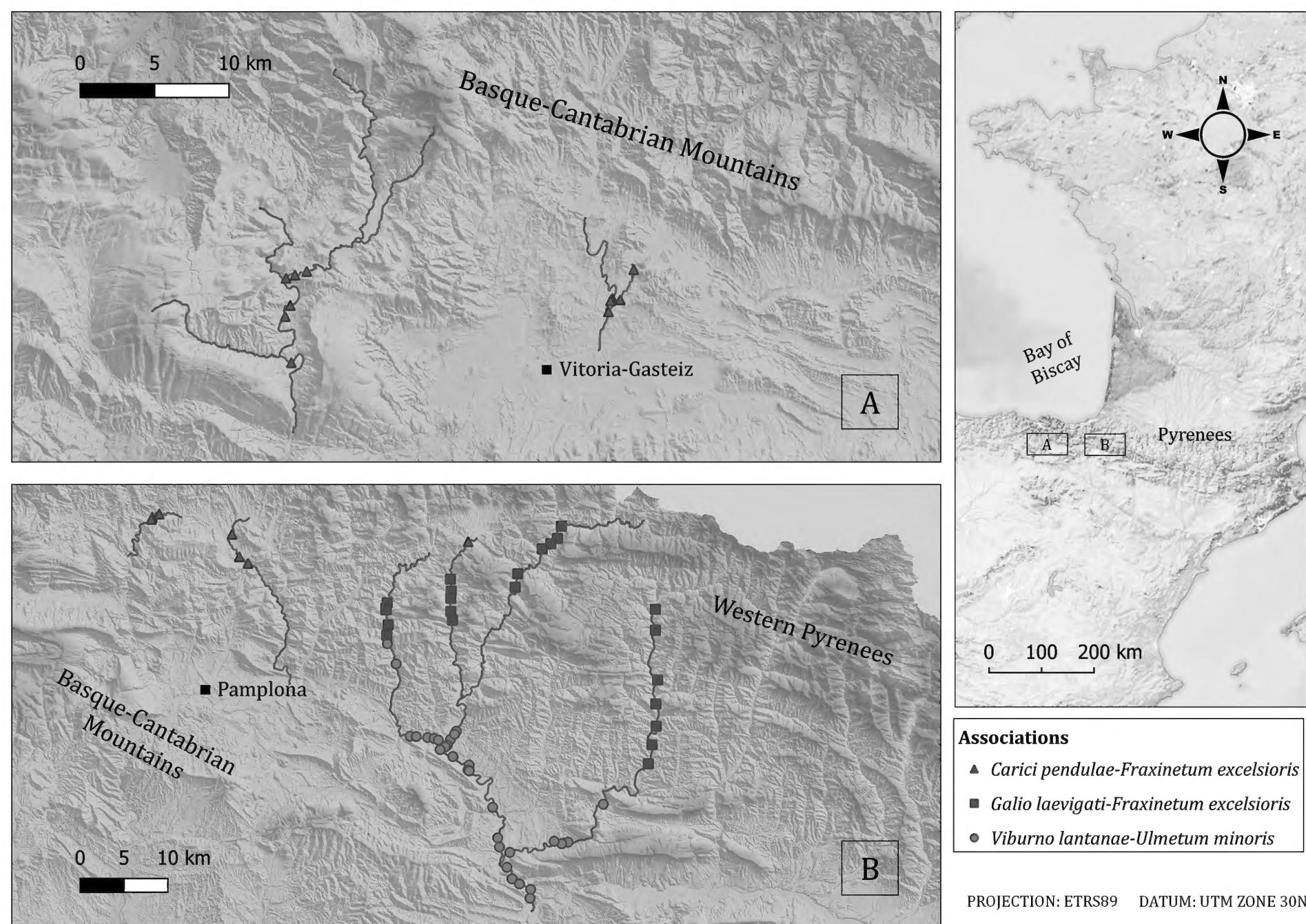
These regions, located in northern Spain, lay on the transition between the temperate and Mediterranean climate, and the whole area shares three biogeographic regions: Atlantic, Alpine and Mediterranean (EEA 2016). The northern part is typically temperate, very oceanic in the coast, with increasing continentality towards the inner subcantabrian valleys and the Pyrenees, the central part is submediterranean, and the southern part is typically Mediterranean (Loidi et al. 2011).

These subcantabrian, submediterranean and western Pyrenean valleys are formed by rivers and streams flowing southwards and eventually joining the Ebro river or one of its tributaries, i.e., all our study area is included in the Ebro basin. From west to east, we sampled riparian forests in the rivers Baia, Zadorra and its tributary Sta. Engracia, Basaburua and Ultzama (Arga basin) and several rivers in Irati basin: Erro, Urrobi, Irati and Zaraitzu (Figure 1). Baia and Zadorra are directly flowing into Ebro river, while Arga and Irati are joining the Pyrenean Aragón river, which is one of the main tributaries of the Ebro. These rivers have their sources in the mountains of the Atlantic-Mediterranean watershed, those from Irati basin in the western Pyrenees and the rest in the Basque-Cantabrian mountains.

The upper and medium sections of these rivers flow under temperate climate and belong to the Atlantic region (subcantabrian valleys) and the Alpine region (western Pyrenean valleys). However, climate in these valleys is drier and more continental than in the Cantabrian valleys

with rivers flowing into the Bay of Biscay (Loidi et al. 2011). The lowest sections of most of these rivers opened gorges through the second chain of Basque-Cantabrian Mountains and the Prepyrenees (the so-called transition mountains) to enter into the Mediterranean region, where they flow under a submediterranean climate. These are the submediterranean valleys, the so-called “transition valleys” (Loidi et al. 2011) in the Basque Country and “central zone” in Navarre (Peralta et al. 2018). The largest submediterranean river sections are located in Irati river basin, where there is also an important gradient in its Pyrenean sections: the Erro and Urrobi rivers, the westernmost ones, are transitional between subcantabrian and Pyrenean valleys, while Zaraitzu river, the easternmost one, is a typical Pyrenean river where spring snow melting has an important role in the water regime. Snow is not an important component in the flowing regime of Atlantic rivers.

The landscape of these valleys is quite diverse, with different forest types as natural vegetation and meadows, scrubs and dry grasslands as semi-natural vegetation. Beech forests are spread in river sources and, depending on the river basin, several forest types can be found in the slopes and valleys. In the subcantabrian valleys (Baia, Zadorra, Sta. Engracia, Basaburua, Ultzama), mesic oak forests with *Quercus robur* occupy the valley bottoms, as well as gentle slopes in the wettest areas, while slopes are occupied by thermophilous deciduous forests (*Quercus faginea*, *Q. pubescens*, *Q. pyrenaica*) (Loidi et



**Figure 1.** Map of the study area showing the location of the 72 plots of floodplain forests sampled in subcantabrian, western Pyrenean and submediterranean valleys of the Basque Country and Navarre.

al. 2011). In the Pyrenean valleys (upper section of Irati basin) the riparian forest directly contacts with the *Q. pubescens* forests, as *Q. robur* is not occurring in the Pyrenean chain. Exceptionally, Irati and Urrobi rivers opened deep gorges in siliceous outcrops of western Pyrenees, and there the riparian forest contacts with *Q. petraea* forests. In the submediterranean valleys (lowest section of Irati basin) the riparian forests are neighbored by *Q. faginea* forests, although, given the intense agricultural use in these valleys, cereal and other crops have become the main contact of riparian forests. Hills and slopes, extensively grazed by sheep, horses, and cattle in the past, are now mostly abandoned (Peralta et al. 2018). In contrast, in the northern sections, the land use is mostly cattle breeding in the valleys and forestry in the mountain slopes.

The riparian vegetation is quite complex in the submediterranean valleys, with slow flowing sections rich in aquatic communities and river deposits colonized by tall-herb communities with *Epilobium hirsutum*, *Mentha longifolia*, *Eupatorium cannabinum*, etc., as well as willow communities with *Salix purpurea*. It is also common that a softwood forest with *Salix alba*, *Alnus glutinosa* and *Populus nigra* develops between the riverbank and the riparian hardwood forest (Peralta et al. 2018). This flooded forest corresponds to the association *Humulo lupuli-Alnetum glutinosae*, described by Biurrun et al. (1994) and included by Biurrun et al. (2016) in the alliance *Popilion albae*. In the subcantabrian valleys there are also some slow flowing sections, but the riparian vegetation complex is not so developed. Tall-herb communities are more fragmentary, and the alder forest growing in the most frequently flooded banks occupies a very narrow space between the hardwood forest and the riverbank, often formed by one line of alder trees, which is absent in the smallest rivers, such as Basaburua river. The western Pyrenean rivers of Irati basin are more torrential, and it is almost impossible to distinguish two different riparian forests in the same river section. As a consequence, alder is a typical component of the hardwood forest, becoming abundant in the topographically most favorable riverbanks. However, alder is totally absent in Zaraitzu river, the most torrential one in the basin, and almost absent from Erro river, the smallest one and with a very low summer flow.

## Methods

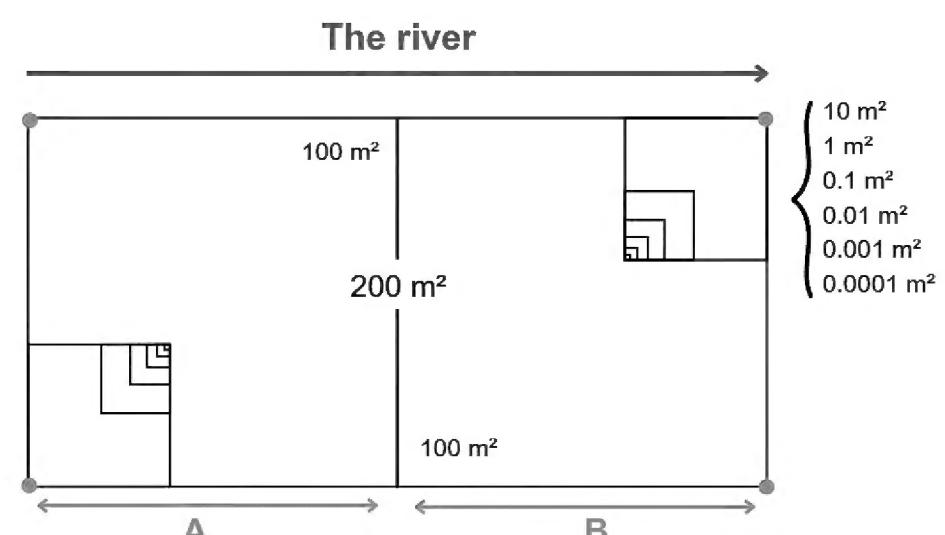
### Vegetation data

The target riparian forests are well represented in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG; EU-00-011, Biurrun et al. 2012), as well as in SIVIM Floodplain forests (EU-00-24; Biurrun and Font 2020), with several hundred plots also available in EVA (Chytrý et al. 2016) and sPlot (Bruelheide et al. 2019) databases. Nevertheless, we conducted a new standardized sampling in order to get a homogeneous dataset formed by high quality plots sharing identical sampling method. The sampling took place mostly in forest patches with historic plots already present in the mentioned databases. These

historic plots were used both in the Iberian syntaxonomical revision of floodplain forests (Biurrun et al. 2016) and the EUNIS habitat classification (Chytrý et al. 2020).

We sampled 72 plots distributed across the study area, 18 in subcantabrian river sections (Baia, Zadorra, Sta. Engracia, Basaburua, Ultzama), 24 in the western Pyrenean sections and 30 in submediterranean sections of Irati basin. Irati basin is the largest and has the largest elevation gradient regarding plot location, from 404 m a.s.l. in the lowest section to 875 m a.s.l. in the upper section of Urrobi river. This elevation gradient is much smaller along the subcantabrian valleys, from 513 m a.s.l. in Zadorra river (near the Basque capital Vitoria-Gasteiz) to 606 m a.s.l. in the highest plot in Baia river.

We adapted to nested sampling in forests the standard EDGG sampling method (Dengler et al. 2016, 2021), which was originally created for the nested sampling of grasslands and other open vegetation types. Due to the specific linear shape of floodplain forests, the biggest plots of the nested series were not squares, but rectangles of 10 m × 20 m. It was not possible to set plots of 20 m × 20 m as many forest patches were not wide enough. Exceptionally, plots were 8 m wide and 25 m long. All 72 plots were set as permanent plots with four red-painted wooden stakes at each corner, along with their respective geographical coordinates. In our adaptation to the forest sampling, we set two contiguous 10 m × 10 m plots parallel to the riverbed trying to include homogeneous forest stands. The herb layer was sampled following the nested sampling design in two series, with subplots replicated once in each. The nested series in the downstream 100 m<sup>2</sup> started in the corner near the river, while the upstream series was located in the inner corner (Figure 2). This nested sampling included all herbaceous plant species as well as woody species seedlings and saplings up to 0.7 m high (Staubli et al. 2021). In the smallest subplots (0.0001 to 10 m<sup>2</sup>) species presence only was recorded. Cover (in %) of species in the herb layer was recorded in the two 100 m<sup>2</sup> plots. The tree and shrub layers were sampled in the 200 m<sup>2</sup> plot (i.e., the two 100 m<sup>2</sup> plots together), where species cover was also estimated as percentage cover. For the multivariate analyses we used floristic data



**Figure 2.** Adaptation of the EDGG nested-plot design (Dengler et al. 2016) for the nested sampling of the herb layer of riparian forests.

of 200 m<sup>2</sup> plots, so we calculated the mean cover of the herb-layer species in both 100 m<sup>2</sup> plots and combined this table with the data of the tree and shrub layers sampled in the 200 m<sup>2</sup> plots, in order to get a complete composition table at the grain size of 200 m<sup>2</sup>.

We estimated the cover of each vegetation layer (tree, shrub, herb and cryptogam) as well as cover of litter, dead wood and fractions of abiotic soil surface in each 200 m<sup>2</sup> plot. Measured parameters and other plot level data are available in Suppl. material 1. The main sampling took place in summer of the years 2022 and 2023, exceptionally in 2024, but we conducted an additional sampling in spring 2023 and 2024 not to dismiss the vernal geophytes. During these spring samplings we recorded the presence and cover in the 200 m<sup>2</sup> plot of vernal species that had not been found in the previous sampling.

## Diversity variables

We calculated the species richness and the Shannon diversity index for each 200 m<sup>2</sup> plot and used these two variables as measures of alpha diversity. We also calculated the species richness of the herb layer for all subplot sizes and, additionally, we calculated Whittaker's beta diversity for each forest type, as the quotient between its gamma diversity and the mean richness at plot level (Whittaker 1960). As a fine-scale beta diversity measure we used the slope parameter of the Species Area Relationship (SAR, Jurasiński et al. 2009). This slope parameter, the *z* value, represents the exponent of the power law function of the SAR (Dembicz et al. 2021a), which has been proposed as the best fitting function among the numerous proposed SAR functions, both in non-nested (as islands, Matthews et al. 2016) and nested (Dengler et al. 2020) sampling units. This *z* value is widely used to compare spatial species turnover between different ecological situations (Drakare et al. 2006; de Bello et al. 2007; Dembic et al. 2021a) or community types (Dembicz et al. 2021b). As *z* value only exhibits a small amount of scale dependence (Zhang et al. 2021), we assumed it to be constant within our range of grain sizes. We calculated the *z* value for each 200 m<sup>2</sup> plot using the means of the two subplots of each size from 0.0001 m<sup>2</sup> to 100 m<sup>2</sup>. All diversity measures at plot level are available in Suppl. material 1.

## Ecological and disturbance indicator values

As proxies of the local-scale site conditions of the plot locations, we selected the Ecological Indicator Values for Europe (EIVE; Dengler et al. 2023) and the Disturbance Indicator Values for European plants (DIV; Midolo et al. 2023). As shown by Scherrer and Guisan (2019), mean ecological indicator values can improve the predictive power of models much compared to using only approximate site conditions from modelled databases via the coordinates. We calculated the plot-wise means for EIVE and DIV using

the data of the entire community. The means of EIVE values were based on presence/absence data (unweighted), while those of DIV values were based on abundance data (community weighted means, CWM). Both calculations were performed with the "cwm" function from the R package *weimea* (Zelený 2020). The values of these indices in each plot are available in Suppl. material 1.

## Climatic data

We retrieved climatic data from WorldClim at 30 arc sec resolution (Fick and Hijmans 2017). We selected five climatic variables from WorldClim which have shown to be meaningful in the context of the SW European forests (Biurrun et al. 2016; González-García et al. 2024): BIO1 (Annual mean temperature), BIO7 (Temperature annual range), BIO10 (Mean temperature of the warmest quarter), BIO12 (Annual precipitation), BIO18 (Precipitation of the warmest quarter) and additionally we calculated the ombrothermic index of the warmest quarter, i.e., the index  $I_{os_3}$  of Rivas-Martínez, which is used to delimit regions under Mediterranean climate (Rivas-Martínez et al. 2011). This index is calculated dividing the sum of the precipitation of the warmest quarter by the sum of the mean monthly temperatures of the warmest quarter ( $BIO18/\sum t_{\text{summer quarter}}$ ). Generally speaking,  $I_{os_3} < 2$  indicates Mediterranean climate. The values of climatic variables for each plot are available in Suppl. material 1.

## Statistical analyses

### *Expert system for automatic classification to EUNIS habitats*

We used the composition data of the 200 m<sup>2</sup> grain size, where records of woody species in different layers were merged using the algorithm by Fischer (2015). The resulting matrix was formed by 72 plots and 456 taxa. We applied the EUNIS-ESy to this matrix in order to classify our plots to habitat types of the EUNIS Habitat classification using the R implementation of the EUNIS-ESy (Bruelheide et al. 2021). We used the latest version of the expert system (Chytrý et al. 2021).

### *Unsupervised classification, ordination and diagnostic species*

We started with the same floristic matrix used for the EUNIS habitat classification, formed by 72 plots and 456 taxa. To reduce noise, we removed species that occurred only in one plot before conducting multivariate analyses (McCune and Grace 2002). This led to the removal of 116 taxa. No taxa were removed in 14 plots, and the rest of plots had few species removed (mostly 1–2, a few 4–8). The most extreme case was one plot of submediterranean riparian forest located near a campsite, with 13 singletons, all of them ruderal species. Bray-Curtis dissimilarity was calculated on the square-root transformed cover of species in plots, and

the resulting distance matrix was used both for the classification and ordination analyses. Bray-Curtis dissimilarity is widely used in vegetation studies due to the relatively equal weighting it gives to both dominant and rare species in analyses (Bray and Curtis 1957), and is considered a robust measure of ecological distance (Faith et al. 1987).

We classified plots by means of agglomerative hierarchical clustering using the Beta flexible linkage method (with  $\beta = -0.25$ ) in *cluster* package (R Core Team 2024). The structure of the resulting dendrogram was used to decide its partition in clusters, supported by the current classification of these forests in the study area. To test significant differences in composition and structure between clusters, we conducted permutational multivariate analysis of variance (PERMANOVA) of these groups using the “adonis2” function in the *vegan* R package with the calculated Bray-Curtis dissimilarity matrix and 999 permutations (Oksanen et al. 2024).

We determined diagnostic species of the resulting clusters using the phi coefficient of association (Chytrý et al. 2002) standardized to equal plot number per cluster (Tichý and Chytrý 2006) in the Ginkgo program of the VEGANA package (De Cáceres et al. 2007). Species with phi  $\geq 0.3$  were considered diagnostic, and those with phi  $\geq 0.5$  highly diagnostic. Additionally, for species to be considered diagnostic, we also required that their constancy in the target cluster was at least 20% and its phi-value at least 0.25 higher than in the cluster with the next-higher phi-value, as in García-Mijangos et al. (2021). Taxa identified only at genus level were removed from the list of diagnostic species. Some species that were highly diagnostic for one cluster and diagnostic for another are indicated as such, provided their phi value as highly diagnostic is  $\geq 0.25$  than their phi value as diagnostic.

To visualize the gradient of vascular plant species composition across the vegetation types, we visualized the clusters in multivariate space using non-metric multidimensional scaling (NMDS; McCune and Grace 2002) ordinations of our species matrix. We created all NMDS ordinations with the R package *vegan* function “metaMDS” using Bray-Curtis dissimilarity and 100 random starts (Oksanen et al. 2024). To assess which climatic gradients and structural parameters were correlated with the results of the NMDS ordination, we projected them onto our ordination using the R package *vegan* function “envfit” with 100 permutations (Oksanen et al. 2024). We projected 15 variables (6 climatic, 8 structural and elevation) but only significant variables ( $p$ -value  $< 0.05$ ) were plotted: litter cover, gravel cover, stones and rocks cover, cryptogam cover and BIO7 (temperature annual range).

### **Analyses of differences between forest types**

Differences among forest types regarding diversity values and structural and bioclimatic variables were analyzed by means of analyses of variance (ANOVAs) in the R programming language (R Core Team 2024). Tukey's post-hoc test was applied following a significant ANOVA ( $p$ -value  $< 0.05$ ). For some variables not meeting the assumption of normal

distribution we performed the non-parametric Kruskal-Wallis test, as well as the post-hoc Dunn test with the Bonferroni correction for significant pairs. To reduce the pitfalls of using CWMs in vegetation analyses, which often provide overly optimistic results (Zelený and Schaffers 2012; Zelený 2018), the differences of EIVE and DIV values among the forest types were analyzed using modified permutation tests with 999 permutations in PRIMER 7 (Clarke et al. 2014).

## **Results**

### **General floristic results**

We identified 456 taxa across all vegetation plots, with only 48 taxa occurring in at least half of the plots ( $\geq 36$ ), and three taxa, *Acer campestre*, *Crataegus monogyna*, and *Hedera hibernica* present in all plots. Among the other most frequent species, the five most common species in the herb layer were *Alliaria petiolata*, *Brachypodium sylvaticum*, *Elymus caninus*, *Geum urbanum*, and *Viola reichenbachiana*, and the five most common woody species *Clematis vitalba*, *Cornus sanguinea*, *Euonymus europaeus*, *Ligustrum vulgare*, and *Rubus caesius*.

Five of the species found were endangered species included in regional catalogues (Boletín Oficial del País Vasco 2011 and Boletín Oficial de Navarra 2023): *Carex strigosa*, *Circaea alpina*, *Galanthus nivalis*, *Lathraea squamaria*, and *Narcissus pseudonarcissus* subsp. *nobilis*. *Galanthus nivalis* is also listed, as Near Threatened, in the European red list of vascular plants (European Commission 2011), and *Narcissus pseudonarcissus* subsp. *nobilis* in the annex II of the EU Habitats Directive (European Union 1992) and the Spanish index of threatened species (Boletín Oficial del Estado 2011). In addition to threatened species, the sampled floodplain forests hosted several Cantabrian-Pyrenean endemics: *Conopodium pyrenaeum*, *Crepis lampsanoides*, *Fritillaria pyrenaica*, *Helleborus viridis* subsp. *occidentalis*, *Meconopsis cambrica*, *Myosotis martini*, *Saxifraga hirsuta*, *Scilla lilio-hyacinthus*, *Scrophularia alpestris*, *Valeriana pyrenaica*, and *Veronica ponae*. Other outstanding species, common in Central European forests and high mountains, but rare in the lowland forests of northern Spain, were *Aconitum napellus* subsp. *vulgaris*, *A. lycoctonum* subsp. *neapolitanum*, *Adenostyles alliariae*, *Anemone ranunculoides*, and *Valeriana officinalis*. Pictures of some of these threatened and endemic species are provided in Figures 3, 4.

Mean species richness per 200 m<sup>2</sup> plot was 75.3, with a minimum of 39 plant species in a submediterranean ash forest dominated by *Fraxinus angustifolia*, with admixture of *Salix alba*, *Alnus glutinosa*, and *Ulmus minor* in the tree layer (IMB10), and a maximum of 124 species in a western Pyrenean ash forest dominated by *Fraxinus excelsior* with *Corylus avellana*, *Alnus glutinosa*, *Fagus sylvatica*, and *Ulmus glabra* (IE03).

Alien species (including archeophytes) were few, 28 species (percentage in the species pool: 6.1%), and none of them were present in more than half of the plots. The most



**Figure 3.** Photos of three taxa included in the red lists of the Basque Country and Navarre: A, *Narcissus pseudonarcissus* subsp. *nobilis*; B, *Lathraea squamaria*; C, *Galanthus nivalis*. Photos A and C by J. Belmonte, B by I. Biurrun.



**Figure 4.** Photos of three species endemic to the Cantabrian-Pyrenean region: A, *Fritillaria pyrenaica*; B, *Meconopsis cambrica*; C, *Scilla lilio-hyacinthus*. Photos A and C by J. Belmonte, B by I. Biurrun.

frequent were *Juglans regia* (27 plots), *Populus nigra* var. *italica* (12) and *Populus ×canadensis* (6), with the following taxa occurring from one to three plots: *Acer platanoides*, *Aesculus hippocastanum*, *Arundo donax*, *Asparagus officinalis*, *Avena sativa*, *Erigeron sumatrensis*, *Ficus carica*, *Fraxinus ornus*, *Helianthus tuberosus*, *Helianthus ×laetiflorus*, *Juglans nigra*, *Ligustrum ovalifolium*, *Malus pumila*, *Oxalis* sp., *Picea abies*, *Populus alba*, *Prunus armeniaca*, *P. laurocerasus*, *Quercus rubra*, *Solanum tuberosum*, *Triticum aestivum*, *Veronica persica*, *Vicia faba*, *Xanthium* sp., and *Yucca gloriosa*. The mean invasion level at plot level was 1.6, with 26 plots without any alien species, and the highest invasion level (6.8) in a submediterranean plot in Irati river.

## Expert system

Only five plots were classified by EUNIS-ESy in habitat T13 (Temperate hardwood riparian forest), nine were classified to habitat T1E (*Carpinus* and *Quercus* mesic deciduous forest), four to habitat T12 (*Alnus glutinosa*-*Alnus incana* forest on riparian and mineral soils), three to T1F (Ravine forest), two to T17 (*Fagus* forest on non-acid soils), and one to T1H (Broadleaved deciduous plantation of non-site-native trees). 39 plots were only classified at

EUNIS level 1 as T (Forests and other wooded land), six plots had multiple assignments at the same hierarchical level, and three did not get a valid assignment to any vegetation type. Among the plots classified in T13, four were submediterranean forests of *Viburno-Ulmetum minoris* (in Irati and Zaraitzu rivers), and one was a subcantabrian forest of *Carici-Fraxinetum excelsioris* in Ultzama river.

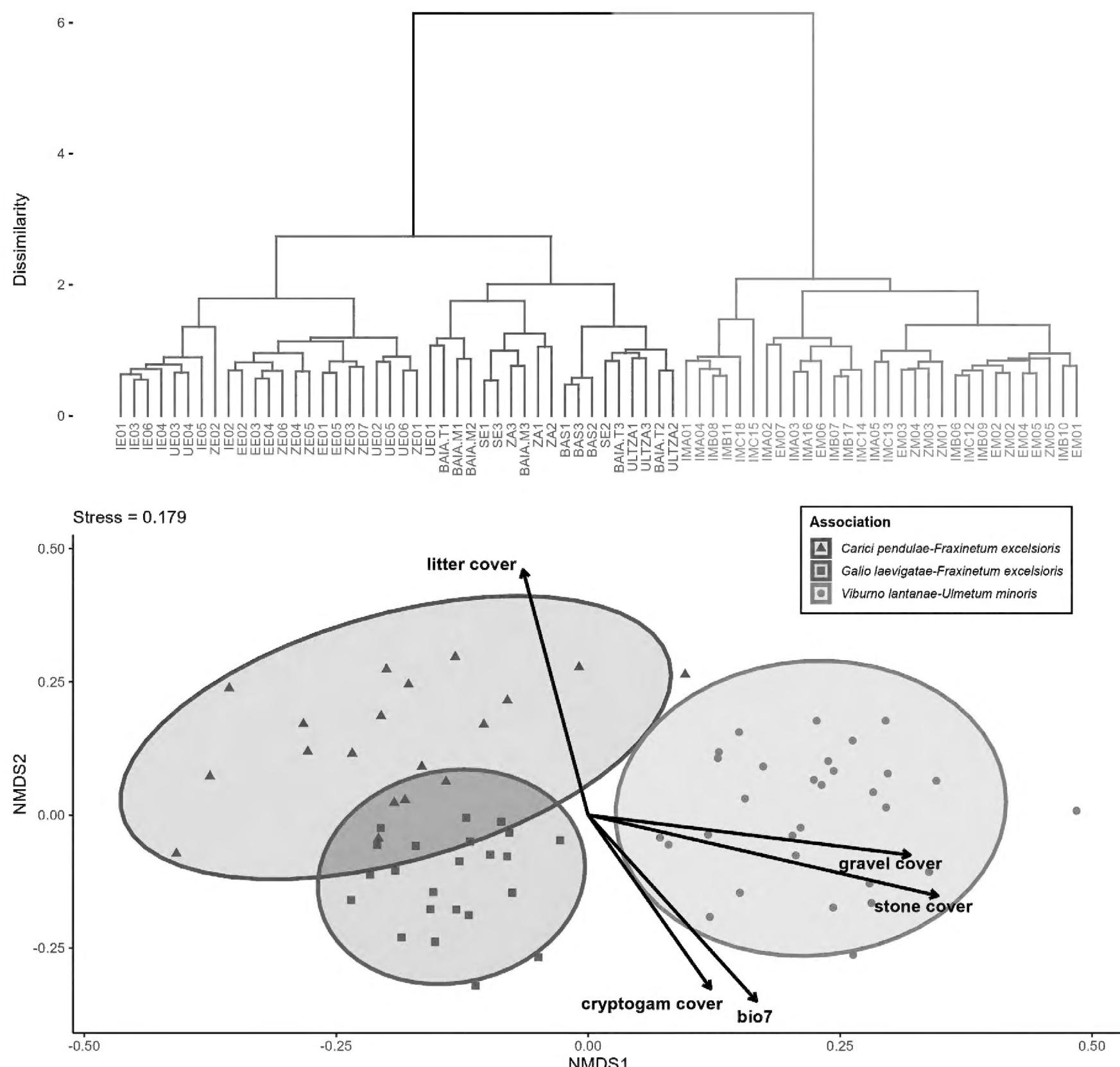
## Floristic differentiation in riparian forests

The agglomerative clustering yielded a dendrogram in which we distinguished three riparian forest types (PERMANOVA  $p < 0.001$ ,  $R^2 = 0.30$ ) (Figure 5). We interpreted these groups as the three associations of the alliance *Alnion incanae* recognized by Biurrun et al. (2016) in the study area: *Carici pendulae-Fraxinetum excelsioris* (subcantabrian riparian forest), *Viburno lantanae-Ulmetum minoris* (submediterranean riparian forest), and *Galio laevigati-Fraxinetum excelsioris* (western Pyrenean riparian forest). In all other results, tables and figures we refer to these three associations. A shortened synoptic table showing the diagnostic species of the three forest types is shown in Table 1, while the full synoptic table is provided in Suppl. material 2.

**Table 1.** Shortened synoptic table of the three associations of hardwood riparian forests in the study area. VU: *Viburno lantanae-Ulmetum minoris*, CF: *Carici pendulae-Fraxinetum excelsioris*, GF: *Galio laevigati-Fraxinetum excelsioris*. Values are percentage frequencies, grey shading indicates  $\phi \geq 0.3$  and dark grey  $\geq 0.5$ . Species are arranged according to decreasing  $\phi$  value. Only species with relative frequency  $> 25\%$  in at least one association are shown. The full synoptic table is available in Suppl. material 2.

Association	VU	CF	GF
Number of plots	30	19	23
<i>Fraxinus angustifolia</i>	100	11	.
<i>Melissa officinalis</i>	73	5	13
<i>Ulmus minor</i>	77	21	9
<i>Juglans regia</i>	73	21	4
<i>Torilis arvensis</i>	67	.	22
<i>Lapsana communis</i>	87	32	43
<i>Calystegia sepium</i>	43	.	4
<i>Quercus faginea</i>	50	11	4
<i>Frangula alnus</i>	37	.	.
<i>Sonchus oleraceus</i>	40	.	4
<i>Anisantha sterilis</i>	30	.	.
<i>Salix alba</i>	30	.	.
<i>Lythrum salicaria</i>	37	11	.
<i>Vitis vinifera</i>	47	.	22
<i>Ligustrum vulgare</i>	97	84	57
<i>Anagallis arvensis</i>	23	.	.
<i>Prunus domestica</i>	67	32	30
<i>Rubia peregrina</i>	57	5	39
<i>Rosa canina</i> aggr.	83	42	65
<i>Solanum dulcamara</i>	27	5	4
<i>Fraxinus excelsior</i>	7	84	100
<i>Quercus robur</i>	.	74	.
<i>Narcissus pseudonarcissus</i> subsp. <i>nobilis</i>	.	68	.
<i>Sambucus nigra</i>	37	100	30
<i>Filipendula ulmaria</i>	3	84	39
<i>Ornithogalum pyrenaicum</i>	.	53	.
<i>Lamium galeobdolon</i>	3	84	61
<i>Glechoma hederacea</i>	23	74	13
<i>Cardamine pratensis</i>	.	53	13
<i>Crataegus laevigata</i>	.	42	.
<i>Aconitum lycoctonum</i> subsp. <i>neapolitanum</i>	.	32	.
<i>Aconitum napellus</i> subsp. <i>vulgare</i>	.	32	.
<i>Arum italicum</i>	50	84	39
<i>Ficaria verna</i>	60	84	26
<i>Mercurialis perennis</i>	.	47	26
<i>Fritillaria pyrenaica</i>	.	26	.
<i>Lamium maculatum</i>	17	58	26
<i>Scilla lilio-hyacinthus</i>	.	42	22
<i>Lilium martagon</i>	.	32	9
<i>Quercus faginea</i> $\times$ <i>robur</i>	7	32	.
<i>Melica uniflora</i>	23	53	100
<i>Veronica chamaedrys</i>	17	47	96
<i>Fagus sylvatica</i>	7	37	87
<i>Moehringia trinervia</i>	3	32	83
<i>Fragaria vesca</i>	.	.	61
<i>Buxus sempervirens</i>	73	.	100
<i>Poa nemoralis</i>	47	42	100
<i>Torilis japonica</i>	17	26	78
<i>Tilia platyphyllos</i>	37	21	87
<i>Bromopsis ramosa</i>	50	53	100
<i>Hepatica nobilis</i>	10	42	78
<i>Geranium phaeum</i>	3	16	61
<i>Silene dioica</i>	.	63	78
<i>Silene vulgaris</i>	13	.	57
<i>Knautia arvernensis</i>	.	16	52
<i>Malus sylvestris</i>	3	.	43
<i>Pulmonaria affinis</i>	.	.	39
<i>Potentilla sterilis</i>	.	37	61
<b>Association</b>			
<b>Number of plots</b>			
<i>Carex sylvatica</i>	43	53	91
<i>Acer opalus</i>	10	.	48
<i>Ulmus glabra</i>	10	16	57
<i>Galium laevigatum</i>	.	.	35
<i>Crepis lampsanoides</i>	7	32	61
<i>Luzula sylvatica</i>	3	21	52
<i>Quercus pubescens</i>	13	.	48
<i>Hieracium murorum</i>	3	5	39
<i>Lathyrus laevigatus</i>	.	.	30
<i>Cerastium fontanum</i>	3	.	35
<i>Milium effusum</i>	7	16	48
<i>Trifolium repens</i>	17	.	48
<i>Saxifraga hirsuta</i>	.	21	43
<i>Clinopodium vulgare</i>	10	.	39
<i>Cruciata laevipes</i>	50	37	83
<i>Vicia sepium</i>	17	42	65
<i>Solidago virgaurea</i>	.	.	26
<i>Veronica montana</i>	40	58	83
<i>Trifolium pratense</i>	37	5	61
<i>Campanula trachelium</i>	37	16	65
<i>Ranunculus acris</i>	60	16	78
<i>Viburnum lantana</i>	67	37	87
<i>Anemone nemorosa</i>	17	5	43
<i>Carex divulsa</i>	17	5	43
<i>Carex flacca</i>	13	11	43
<i>Festuca rubra</i> aggr.	3	.	26
<i>Veronica ponae</i>	3	.	26
<i>Aquilegia vulgaris</i>	10	11	39
<i>Viburnum opulus</i>	13	32	52
<i>Euphorbia amygdaloides</i>	77	63	96
<i>Equisetum arvense</i>	33	21	61
<i>Deschampsia cespitosa</i>	57	32	78
<i>Saponaria officinalis</i>	10	.	30
<i>Primula veris</i>	7	21	39
<i>Myosotis martini</i>	.	11	26
<i>Stachys sylvatica</i>	27	26	57
<b>Other diagnostic species of the class <i>Alno-Populetae</i>:</b>			
<i>Acer campestre</i>	100	100	100
<i>Hedera hibernica</i>	100	100	100
<i>Brachypodium sylvaticum</i>	100	95	100
<i>Alliaria petiolata</i>	90	95	100
<i>Geum urbanum</i>	87	100	100
<i>Elymus caninus</i>	97	74	100
<i>Rubus caesius</i>	100	79	91
<i>Clematis vitalba</i>	93	63	100
<i>Galium aparine</i>	93	95	43
<i>Dioscorea communis</i>	70	74	48
<i>Schedonorus giganteus</i>	47	63	65
<i>Carex pendula</i>	60	47	30
<i>Heracleum sphondylium</i>	47	53	39
<i>Urtica dioica</i>	37	58	39
<i>Alnus glutinosa</i>	47	32	39
<i>Circaea lutetiana</i>	30	26	57
<i>Sympytum tuberosum</i>	20	53	35
<i>Fraxinus angustifolia</i> $\times$ <i>excelsior</i>	30	47	4
<i>Angelica sylvestris</i>	23	11	35
<i>Carex remota</i>	13	32	30
<i>Conopodium pyrenaeum</i>	3	95	78
<i>Primula elatior</i>	.	63	65
<i>Isopyrum thalictroides</i>	.	53	43
<i>Chaerophyllum temulum</i>	30	.	26
<i>Iris foetidissima</i>	30	32	.
<i>Allium ursinum</i>	.	42	26
<i>Populus nigra</i>	30	5	9
<i>Clinopodium menthifolium</i>	27	.	13
<i>Humulus lupulus</i>	17	26	.
<b>Other species:</b>			
<i>Crataegus monogyna</i>	100	100	100
<i>Cornus sanguinea</i>	100	84	100
<i>Viola reichenbachiana</i>	80	100	100

Association	VU	CF	GF	Association	VU	CF	GF
Number of plots	30	19	23	Number of plots	30	19	23
<i>Euonymus europaeus</i>	70	100	96	<i>Hypericum perforatum</i>	43	16	43
<i>Geranium robertianum</i>	77	95	74	<i>Orobanche hederae</i>	50	16	35
<i>Corylus avellana</i>	53	95	100	<i>Ranunculus repens</i>	30	26	39
<i>Rosa arvensis</i>	43	95	96	<i>Lathraea clandestina</i>	40	21	9
<i>Taraxacum</i> sp.	90	37	83	<i>Melilotus albus</i>	30	.	39
<i>Rubus ulmifolius</i>	77	53	57	<i>Picris hieracioides</i>	27	.	43
<i>Lonicera xylosteum</i>	57	58	74	<i>Arrhenatherum elatius</i>	27	.	39
<i>Viola hirta</i>	67	53	57	<i>Galeopsis tetrahit</i>	7	32	39
<i>Anthriscus sylvestris</i>	40	58	61	<i>Eupatorium cannabinum</i>	20	11	35
<i>Dactylis glomerata</i>	60	32	70	<i>Hesperis matronalis</i>	3	37	35
<i>Arctium minus</i>	67	32	48	<i>Medicago</i> sp.	30	.	30
<i>Prunus spinosa</i>	33	58	70	<i>Plantago major</i>	30	.	26
<i>Helleborus viridis</i>	3	84	83	<i>Poa trivialis</i>	20	16	26
<i>Prunella vulgaris</i>	70	11	57	<i>Allium oleraceum</i>	30	.	17
<i>Stellaria holostea</i>	7	79	74	<i>Veronica hederifolia</i>	17	32	9
<i>Agrostis stolonifera</i>	53	32	43	<i>Chaerophyllum aureum</i>	17	.	30
<i>Rhamnus cathartica</i>	47	42	39	<i>Cardamine flexuosa</i>	3	21	26
<i>Lonicera periclymenum</i>	37	47	30	<i>Hippocrepis emerus</i>	13	.	30
<i>Ruscus aculeatus</i>	27	58	35	<i>Ilex aquifolium</i>	.	21	30
<i>Acer pseudoplatanus</i>	30	53	30	<i>Oxalis acetosella</i>	3	26	22
<i>Ajuga reptans</i>	10	58	52	<i>Populus pyramidalis</i>	27	.	13
<i>Helleborus foetidus</i>	40	11	52	<i>Brachypodium rupestre</i>	3	16	26



**Figure 5.** Dendrogram with the three forest types produced by the agglomerative hierarchical clustering of 72 plots (above). The three groups were supported by PERMANOVA ( $p < 0.001$ ,  $R^2 = 0.30$ ). NMDS ordination diagram with the structural and climatic variables significantly correlated with the ordination plotted (below).

The western Pyrenean association *Galio laevigati-Fraxinetum excelsioris* included 60 diagnostic species, 16 of them highly diagnostic. The species with highest diagnostic value were common species in mesic forests, like *Melica uniflora*, *Veronica chamaedrys*, *Fagus sylvatica* and *Moehringia trinervia*. This association also included some diagnostic species that have a Pyrenean distribution in Spain such as *Acer opalus*, *Cardamine heptaphylla*, *Galium laevigatum*, *Geranium phaeum*, and *Pulmonaria affinis*. The other two associations included far fewer diagnostic species. *Viburno lantanae-Ulmetum minoris* had 23 diagnostic species, only six of them highly diagnostic. The most important was *Fraxinus angustifolia*, which only occurs in this submediterranean association within Iberian communities belonging to the *Alnion incanae*. *Ulmus minor* was also highly diagnostic, as well as some ruderal species as *Lapsana communis*, *Melissa officinalis*, and *Torilis arvensis*. The subcantabrian riparian forest of the association *Carici pendulae-Fraxinetum excelsioris* had 20 diagnostic species, nine of them highly diagnostic. *Quercus robur* stands out, as it is absent from both Pyrenean and submediterranean valleys. It is also remarkable the high diagnostic value of several geophytes and hemicryptophytes typical from wet grasslands and forests, such as *Filipendula ulmaria*, *Narcissus pseudonarcissus* subsp. *nobilis*, *Ornithogalum pyrenaicum*, *Aconitum napellus* subsp. *vulgare*, and *A. lycoctonum* subsp. *neapolitanum*, some of them indicated as diagnostic species of the alliance *Alnion incanae* by Biurrun et al. (2016). *Fraxinus excelsior* separates the subcantabrian and western Pyrenean forests from the submediterranean one, as it was moderately diagnostic in *Carici-Fraxinetum* and highly diagnostic in *Galio-Fraxinetum*. Both associations also shared other nemoral species such as *Conopodium pyrenaeum*, *Helleborus viridis* subsp. *occidentalis*, *Isopyrum thalictroides*, and *Stellaria holostea*, as well as *Primula elatior*, typical species of riparian forests. Pictures of these forests are provided in Figures 6, 7.



**Figure 6.** Vernal aspect of the ground layer in a forest stand of the *Carici pendulae-Fraxinetum excelsioris* (Baia river). Photo: J. Belmonte.

## Diversity patterns

Submediterranean forests of the *Viburno-Ulmetum minoris* had the highest Whittaker's beta diversity (4.7), which was considerably lower in the *Fraxinus excelsior*-dominated forests, with lowest values in the subcantabrian forests of the *Carici-Fraxinetum excelsioris* (3.2) (Table 2). *Carici-Fraxinetum* and *Viburno-Ulmetum* shared the same fine-grain within plot beta diversity in the herb layer, measured as the mean *z* value of the nested plots for each forest type. This value was highest in the western Pyrenean forests of the *Galio-Fraxinetum excelsioris*, but differences were not significant after the post-hoc Dunn test with Bonferroni correction (Figure 8).

Regarding plot-level alpha diversity, species richness and Shannon diversity significantly differed among the three forest types (Table 2). Stands of the *Galio-Fraxinetum* contained significantly more species of vascular plants than stands of the *Carici-Fraxinetum* and the *Viburno-Ulmetum*, while Shannon diversity was significantly lower in *Viburno-Ulmetum* than in *Galio-Fraxinetum* and *Carici-Fraxinetum* (Figure 8).

Table 3 shows the species richness of the herb layer across grain sizes, with significant differences for sizes  $\geq 0.1 \text{ m}^2$ . In all sizes from  $0.1 \text{ m}^2$  to  $200 \text{ m}^2$  richness was highest in *Galio-Fraxinetum* and lowest in *Viburno-Ulmetum minoris*. The higher species richness of *Galio-Fraxinetum* was especially significant for the biggest sizes, from 10 to  $200 \text{ m}^2$ , while for  $0.1$  and  $1 \text{ m}^2$  these differences were only significant when compared to the richness of *Viburno-Ulmetum*.



**Figure 7.** Late-spring view from outside of a stand belonging to the *Viburno lantanae-Ulmetum minoris* (Iraty river). Photo: I. Biurrun.

**Table 2.** Mean values of diversity indices, structural and climatic variables, and ecological and disturbance indicator values in the three forest types. GF: *Galio laevigati-Fraxinetum excelsioris*, CF: *Carici pendulae-Fraxinetum excelsioris*, VU: *Viburno lantanae-Ulmetum minoris*. The column "Test" indicates the analysis applied to test differences among forest types, and the column "Stat." the value of the statistics of the ANOVA, Kruskal-Wallis or Permutation tests. Different letters in mean values indicate significant between-pair differences after significant ANOVA, Kruskal-Wallis or Permutation tests.

	GF n = 23	CF n = 19	VU n = 30	Test	Stat.	p-value
Gamma diversity	308	207	319			
Whittaker's $\beta$	3.37	3.10	4.68			
Species richness	91.8 $\pm$ 17.3 (a)	66.8 $\pm$ 20.3 (b)	68.2 $\pm$ 15.9 (b)	Kruskal-Wallis	21.02	< 0.001
Shannon diversity index	2.54 $\pm$ 0.22 (a)	2.63 $\pm$ 0.15 (a)	2.33 $\pm$ 0.23 (b)	ANOVA	25.18	< 0.001
z value	0.32 $\pm$ 0.05 (a)	0.29 $\pm$ 0.05 (a)	0.29 $\pm$ 0.05 (a)	Kruskal-Wallis	6.22	0.04
Elevation (m a.s.l.)	671 $\pm$ 55 (b)	568 $\pm$ 80 (a)	460 $\pm$ 38 (c)	Kruskal-Wallis	56.56	< 0.001
Tree layer cover (%)	84 $\pm$ 13	88 $\pm$ 9	87 $\pm$ 10	Kruskal-Wallis	0.53	0.769
Shrub layer cover (%)	52 $\pm$ 22	50 $\pm$ 16	47 $\pm$ 21	ANOVA	0.48	0.619
Herb layer cover (%)	74 $\pm$ 17	83 $\pm$ 13	76 $\pm$ 16	Kruskal-Wallis	4.53	0.104
Cryptogam layer cover (%)	25 $\pm$ 23 (b)	3 $\pm$ 5 (a)	5 $\pm$ 8 (a)	Kruskal-Wallis	18.22	< 0.001
Litter cover (%)	32 $\pm$ 17 (b)	54 $\pm$ 20 (a)	43 $\pm$ 22 (ab)	Kruskal-Wallis	10.01	0.006
Dead wood cover (%)	9 $\pm$ 5 (b)	6 $\pm$ 5 (a)	10 $\pm$ 6 (b)	Kruskal-Wallis	8.35	0.01
Stones and rocks cover (%)	11 $\pm$ 20 (b)	1 $\pm$ 2 (a)	4 $\pm$ 9 (a)	Kruskal-Wallis	16.80	< 0.001
Gravel cover (%)	7 $\pm$ 10 (b)	0 $\pm$ 0 (a)	3 $\pm$ 9 (a)	Kruskal-Wallis	17.55	< 0.001
BIO1 ( $^{\circ}$ C)	11.0 $\pm$ 0.5 (a)	11.2 $\pm$ 0.4 (a)	12.5 $\pm$ 0.4 (b)	Kruskal-Wallis	50.92	< 0.001
BIO12 (mm)	930 $\pm$ 61 (a)	928 $\pm$ 89 (a)	773 $\pm$ 56 (b)	ANOVA	46.37	< 0.001
BIO7 ( $^{\circ}$ C)	24.3 $\pm$ 0.5 (a)	23.7 $\pm$ 0.6 (a)	26.0 $\pm$ 0.5 (b)	Kruskal-Wallis	51.17	< 0.001
BIO10 ( $^{\circ}$ C)	18.1 $\pm$ 0.6 (a)	17.9 $\pm$ 0.5 (a)	20.0 $\pm$ 0.5 (b)	Kruskal-Wallis	50.57	< 0.001
BIO18 (mm)	158 $\pm$ 11 (a)	158 $\pm$ 19 (a)	128 $\pm$ 8 (b)	Kruskal-Wallis	48.14	< 0.001
los <sub>3</sub>	2.92 $\pm$ 3.04 (a)	2.94 $\pm$ 3.71 (a)	2.14 $\pm$ 1.90 (b)	Kruskal-Wallis	49.24	< 0.001
Disturbance frequency	0.13 $\pm$ 0.04 (a)	0.12 $\pm$ 0.03 (a)	0.17 $\pm$ 0.04 (b)	Permutation	15.40	< 0.001
Disturbance frequency herb layer	1.35 $\pm$ 0.02 (a)	1.35 $\pm$ 0.01 (a)	1.39 $\pm$ 0.03 (b)	Permutation	31.78	< 0.001
Disturbance severity	0.67 $\pm$ 0.01 (ab)	0.68 $\pm$ 0.01 (a)	0.67 $\pm$ 0.01 (b)	Permutation	4.02	0.022
Disturbance severity herb layer	0.20 $\pm$ 0.02 (a)	0.20 $\pm$ 0.02 (a)	0.24 $\pm$ 0.03 (b)	Permutation	33.39	< 0.001
EIVE_Moisture	4.62 $\pm$ 0.19	4.74 $\pm$ 0.13	4.65 $\pm$ 0.25	Permutation	1.95	0.15
EIVE_Nitrogen	5.60 $\pm$ 0.22 (a)	5.89 $\pm$ 0.19 (b)	5.85 $\pm$ 0.26 (b)	Permutation	10.87	< 0.001
EIVE_Reaction	6.45 $\pm$ 0.16 (a)	6.43 $\pm$ 0.13 (a)	6.68 $\pm$ 0.10 (b)	Permutation	30.20	< 0.001
EIVE_Light	5.32 $\pm$ 0.28 (a)	5.17 $\pm$ 0.20 (a)	5.80 $\pm$ 0.31 (b)	Permutation	35.97	< 0.001

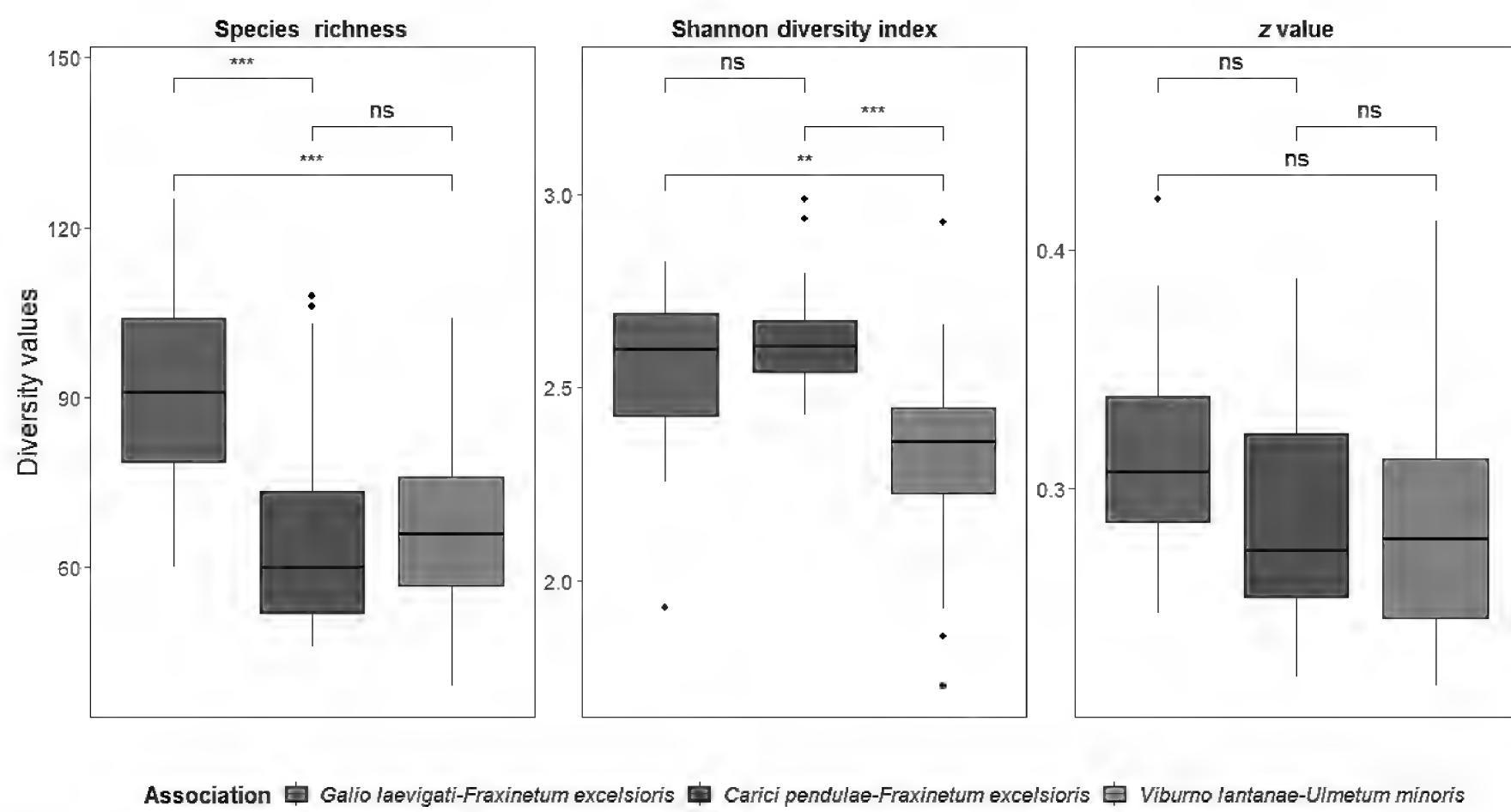
**Table 3.** Scale-dependent diversity patterns of the herb layer in the three associations. GF: *Galio laevigati-Fraxinetum excelsioris*, CF: *Carici pendulae-Fraxinetum excelsioris*, VU: *Viburno lantanae-Ulmetum minoris*. The column "Test" indicates the analysis applied to test differences among forest types, and the column "Stat." the value of the statistics of the ANOVA or Kruskal-Wallis tests. Different letters in mean values indicate significant between-pair differences after significant ANOVA or Kruskal-Wallis analysis.

Plot size (m <sup>2</sup> )	GF n = 23	GF n = 19	VU n = 30	Test	Stat.	p-value
0.0001	1.2 $\pm$ 0.7	1.1 $\pm$ 0.6	1.3 $\pm$ 0.6	Kruskal-Wallis	0.54	0.76
0.001	2.0 $\pm$ 1.2	1.9 $\pm$ 0.8	1.7 $\pm$ 0.8	Kruskal-Wallis	1.29	0.53
0.01	3.6 $\pm$ 1.9	3.9 $\pm$ 1.4	2.9 $\pm$ 1.2	Kruskal-Wallis	4.74	0.09
0.1	8.2 $\pm$ 3.3 (a)	7.7 $\pm$ 2.6 (ab)	5.7 $\pm$ 2.4 (b)	Kruskal-Wallis	12.60	0.002
1	19.5 $\pm$ 6.8 (a)	14.8 $\pm$ 4.4 (ab)	12.1 $\pm$ 4.6 (b)	Kruskal-Wallis	19.22	< 0.001
10	37.3 $\pm$ 8.1 (a)	27.6 $\pm$ 8.7 (b)	23.6 $\pm$ 6.5 (b)	ANOVA	21.43	< 0.001
100	68.1 $\pm$ 13.2 (a)	49.3 $\pm$ 14.7 (b)	46.8 $\pm$ 12.5 (b)	ANOVA	18.48	< 0.001
200	85.4 $\pm$ 16.4 (a)	64.9 $\pm$ 20.9 (b)	60.4 $\pm$ 15.6 (a)	Kruskal-Wallis	20.68	< 0.001

### Structural and climatic variables

As mentioned before, cryptogam cover, litter cover, gravel cover, stone cover and BIO7 were the only structural and climatic variables significantly correlated with the results of the NMDS ordination (Figure 5). According to the analyses of variance, the most outstanding difference among

the forest types regarding their structure was the more than five-fold higher mean cover of the cryptogam layer in the *Galio-Fraxinetum* vs. *Viburno-Ulmetum*, where the cryptogam layer was also considerably more developed than in *Carici-Fraxinetum*, but without significant differences. Litter and dead wood cover also varied across forest types, with highest values for litter and lowest for



Association ■ *Galio Iaevigati-Fraxinetum excelsior* ■ *Carici pendulae-Fraxinetum excelsior* ■ *Viburno lantanae-Ulmetum minoris*

**Figure 8.** Box plots of diversity parameters showing the post-hoc Tukey's post-hoc or Dunn's multiple comparison test with Bonferroni correction, where 'ns' indicates non-significant differences, while significant differences are indicated by \*\* ( $p < 0.01$ ) and \*\*\* ( $p < 0.001$ ).

dead wood in the *Carici-Fraxinetum* (Table 2), although differences were only slightly significant. Regarding the fractions of soil surface, there were significant differences among forest types, especially between *Galio-Fraxinetum*, where cover of stones, rocks and gravel were highest, and the other two forest types, among which *Viburno-Ulmetum* also showed higher cover of rocks, stones and gravel than *Carici-Fraxinetum*, but without significant differences.

Climatic variables also significantly varied across the three forest types. The warmest mean annual temperature and the lowest annual precipitation were recorded in *Viburno-Ulmetum*, which was also subject to the highest annual temperature range and the warmest and driest summer (Table 2). The two temperate ash forests shared climatic features, and their summer ombrothermic index ( $Ios_3$ ) was clearly over 2, while the submediterranean forests of *Viburno-Ulmetum* had a mean  $Ios_3$  of 2.14 (Table 2), significantly lower than in the temperate forests, and close to the threshold that defines the Mediterranean climate ( $Ios_3 < 2$ ).

### Ecological and disturbance indicator values

All ecological indicator values analyzed, except moisture, showed significant differences among forest types (Table 2). *Galio-Fraxinetum* had significantly fewer nitrogen than *Carici-Fraxinetum* and *Viburno-Ulmetum*, while pH and light were significantly higher in *Viburno-Ulmetum* than in *Carici-Fraxinetum* and *Galio-Fraxinetum* (Figure 9).

Disturbance frequency of the whole forest and of the herb layer were highest in *Viburno-Ulmetum*, with significant differences with *Carici-Fraxinetum* and *Galio-Fraxinetum*. Regarding the disturbance severity, the highest differences among forest types were for the herb layer,

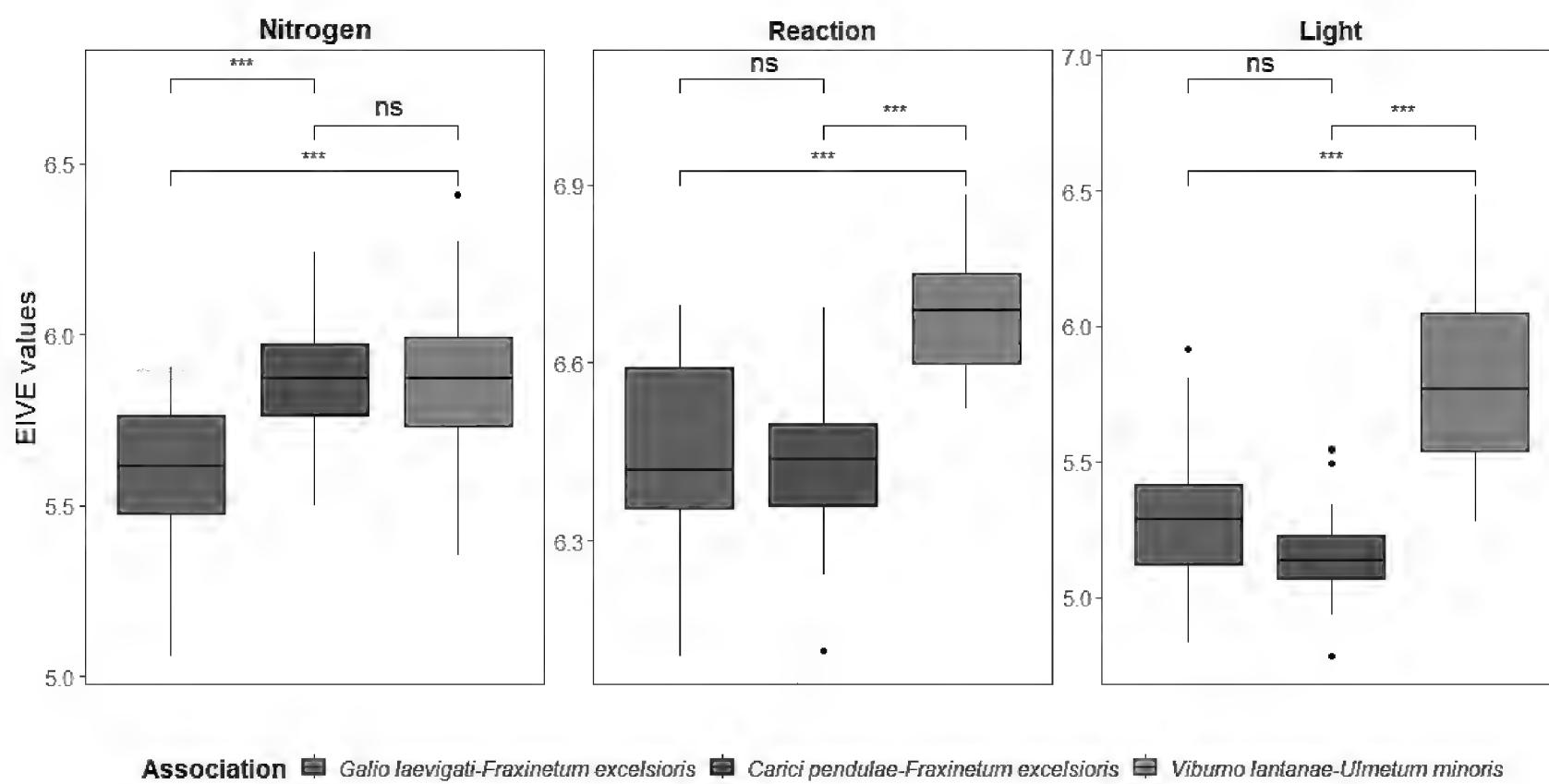
once again with the highest values in *Viburno-Ulmetum* (Table 2, Figure 10).

## Discussion

We have sampled 72 vegetation plots following a standardized protocol including the establishment of permanent plots and a nested sampling design. Many of these plots have been sampled in the same location as historical plots and have been included in ReSurvey database (Knollová et al. 2024). All of them will allow for future monitoring of these habitats.

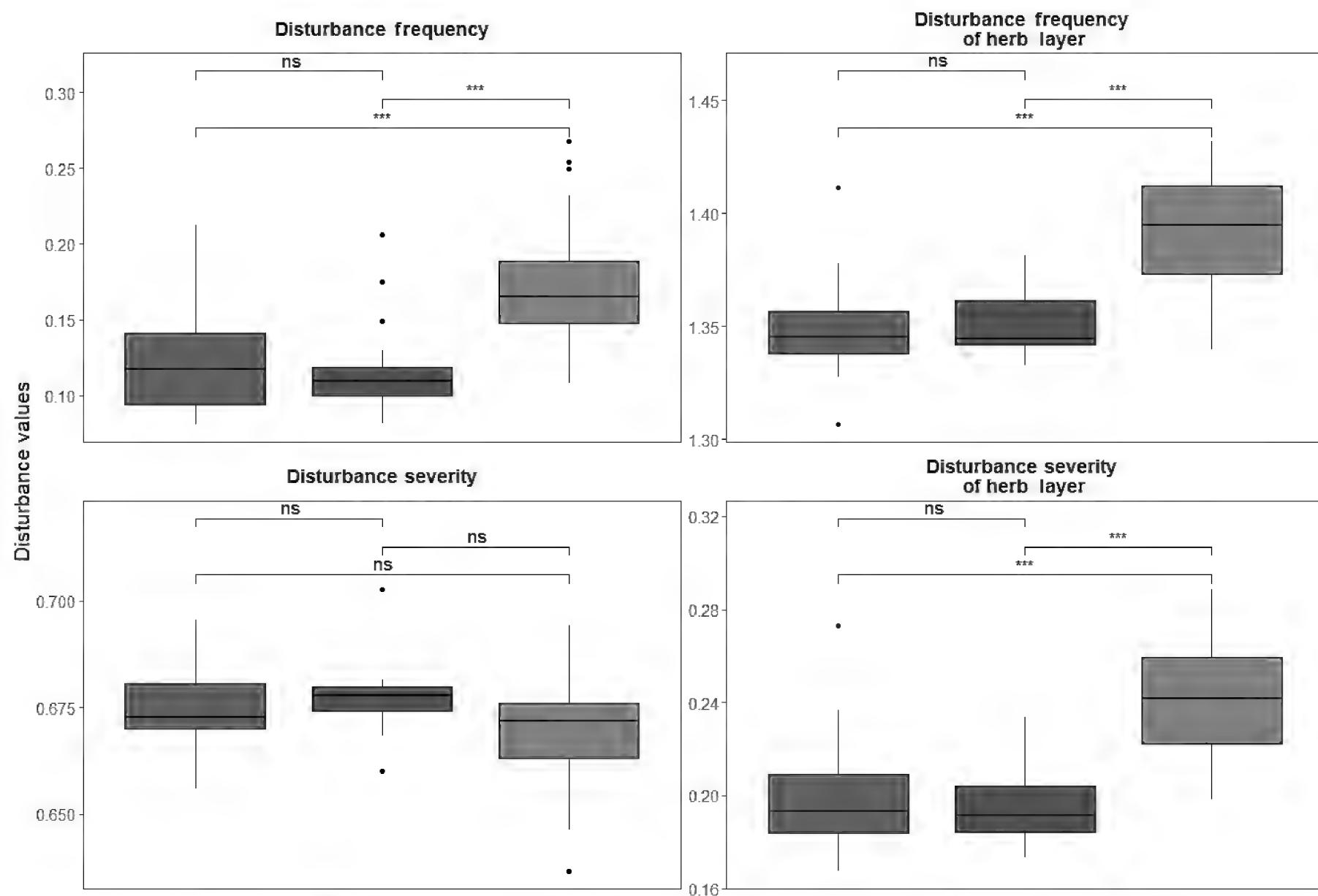
### Nested sampling in forests

To our knowledge, only a few studies have tried nested sampling designs for plant diversity assessment in forests, besides the classical Whittaker plots (Schmid 1984; Stohlgren et al. 1995), where different grain-sizes are independent and non-overlapping, so nestedness is not perfect. The sampling design used in MONITO Project (Chiarucci et al. 1996) does fit a perfect nesting, with non-independent plots ranging from 1 m<sup>2</sup> to 2500 m<sup>2</sup>. Other nested-sampling designs in forests include the nested plot series used by Qiao et al. (2012) in Chinese forests, with plot sizes ranging from 0.25 m<sup>2</sup> to 0.5 ha. In our opinion, the size range used in the two mentioned nested plot designs is not applicable in all forest types, especially in riparian forests, where one can hardly find forest patches big enough to lay 50 m × 50 m plots and even less 70 m × 70 m plots. Staubli et al. (2021) resurveyed forest nested plot series formed by three concentric circles of 30 m<sup>2</sup>, 200 m<sup>2</sup> and 500 m<sup>2</sup>.



**Association** ■ *Galio laevigati-Fraxinetum excelsioris* ■ *Carici pendulae-Fraxinetum excelsioris* ■ *Viburno lantanae-Ulmetum minoris*

**Figure 9.** Box plots of unweighted community means of Ecological Indicator Values for Europe showing the results of the permutation tests, where 'ns' indicates non-significant differences, while significant differences are indicated by \*\* ( $p < 0.01$ ) and \*\*\* ( $p < 0.001$ ).



**Association** ■ *Galio laevigati-Fraxinetum excelsioris* ■ *Carici pendulae-Fraxinetum excelsioris* ■ *Viburno lantanae-Ulmetum minoris*

**Figure 10.** Box plots of community weighted means of Disturbance Indicator Values for European plants showing the results of the permutation tests, where 'ns' indicates non-significant differences, while significant differences are indicated by \*\* ( $p < 0.01$ ) and \*\*\* ( $p < 0.001$ ).

This pattern is more suited to small forest patches, but the circular shape is difficult to fit within the linear form of riparian forests. Another important difference is that the mentioned protocols included all vegetation layers in the nested sampling, while ours was limited to the herb layer.

## General floristic patterns

Our dataset includes 456 vascular plant taxa, some of them rare or endangered species in the region with their few populations often sheltered in these hardwood

riparian forests (Bañares et al. 2004; Uribe-Echebarría and Campos 2006). The mean species richness per 200 m<sup>2</sup>-plot is 75.3, clearly higher than the richness predicted by Večeřa et al. (2019) for deciduous forests of this region at 400 m<sup>2</sup> (see figure S2.8 in Večeřa et al. 2019), but within or a bit higher than the range of the input data used for modelling (see figure S1.1 in Večeřa et al. 2019). These results confirm the northern part of the Iberian Peninsula as a secondary biodiversity hotspot for European deciduous forests, after the main hotspots in Central and south-eastern European mountain ranges, the lowland forests of the hemiboreal zone and the Carpathian foothills (Večeřa et al. 2019).

Alien plant invasions are often favored in sites with increased soil nutrient availability (Davis et al. 2000) and have repeatedly been reported as a major issue in riparian ecosystems from the global to the regional scale (Richardson et al. 2007; Schnitzler et al. 2007; Campos et al. 2013), where they are particularly favored, at the regional level, by additional human disturbance, including infrastructures, agricultural fields, and forest plantations (Liendo et al. 2016; Wagner et al. 2021). However, alien plant invasion is not for the moment a big issue in these subcantabrian, western Pyrenean and submediterranean floodplain forests of northern Spain, with the most frequent alien species being archeophytes (*Juglans regia* and *Populus nigra* var. *italica*).

At a European level, however, temperate hardwood riparian forests are among the top-six most invaded forest habitats (Wagner et al. 2017), with a percentage of alien species in the species pool of 8.9%, while in our dataset this percentage is 6.1%. It is interesting to highlight that the percentage of alien species in the species pool reaches 15.7% in the nearby Cantabrian streams (Liendo et al. 2021), where the riparian forest corresponds to the habitat T12 (*Alnus glutinosa-Alnus incana* forest on riparian and mineral soils). These Cantabrian riparian forests also show a much higher invasion level at plot-level (6.8%) than our target forests in the inner Basque-Navarran valleys (1.6%), which have a quite similar value to European hardwood forests (1.8%). This big difference might be due to several factors, 1) low temperatures constraining the spread of alien species (Svitková et al. 2024), as many alien species common in Cantabrian riparian forests have a subtropical origin (Liendo et al. 2015) and are not adapted to the frequent frosts subcantabrian and submediterranean valleys undergo; 2) dispersal limitation, as invasive species common in Central European forests and thus are adapted to colder environments did not reach northern Spain (Kalusová et al. 2024); and last, but not least 3) lower anthropogenic disturbance of inner valleys comparing to the highly populated and industrialized Cantabrian valleys (Liendo et al. 2015). It might be that there is potentially a high invasion debt in these northern Iberian hardwood riparian forests (Rouget et al. 2016). Wagner et al. (2021) hypothesized that invasion debt is actually more prominent in southern European woodlands.

## EUNIS expert system

Our results after the application of the EUNIS-ESy are quite surprising, especially if we consider that 39 plots were only classified at the level 1, and nine were not classified to a unique level 3 habitat, that is, more than half of the plots were not classified at EUNIS level 3. We repeated the procedure in Juice (Tichý 2002), but results were similar, with only slight changes. Even if we consider that the application of the EUNIS expert system at a regional scale might produce some misclassifications due to the optimization of habitat definition for the whole of Europe (Chytrý et al. 2020) it becomes quite evident that the system needs further adjustment. It is not acceptable that more than half of the plots are not classified at level 3 as this is an impediment for the application of the expert system at the regional scale.

González-García et al. (2024) combined the application of the EUNIS-ESy with unsupervised and semi-supervised methods to classify 4,361 plots of all forest types from the Cantabrian Mixed Forest Ecoregion, and eventually obtained 24 habitat types at EUNIS level 4. Although the EUNIS-ESy classified some plots in habitat T13, the authors do not indicate how many they were and to which associations they belonged to, and reclassified them in the regional level 4 units T111, T121, and T1E1 within T11 (Temperate *Salix* and *Populus* riparian forest), T12 (*Alnus glutinosa-Alnus incana* forest on riparian and mineral soils), and T1E (*Carpinus* and *Quercus* mesic deciduous forest), respectively. These results are comparable with those from the present study, as most of the plots classified at level 3 were included in habitats T1E, T12 and T13.

## Syntaxonomy

The classification of riparian forests in the study area at association level agrees with the framework provided by Biurrun et al. (2016) in their survey of the entire Iberian Peninsula. Three clearly distinct associations are identified: *Galio laevigati-Fraxinetum excelsioris* for the temperate forests from the western Pyrenean valleys, *Carici pendulae-Fraxinetum excelsioris* for the temperate forests from the subcantabrian valleys, and *Viburno lantanae-Ulmetum minoris* for the *Fraxinus angustifolia*-dominated forests in the submediterranean valleys. *Galio-Fraxinetum excelsioris* was described as a new association by Biurrun et al. (2016), who selected a relevé sampled in Zaraitzu river as holotype. This type lacks alder, which is absent in this river probably due to its torrential regime (Peralta et al. 2018); nevertheless, alder is present in forests of this association in the rivers Irati and Urrobi, where it is a common component of the tree layer.

The association *Carici pendulae-Fraxinetum excelsioris* was formally described by Biurrun and García-Mijangos (2002a) to include ash forests from the subcantabrian rivers and streams in the Basque Country and Navarre. The association was first provisionally published by Biurrun (1999) with six relevés from Basaburua and other

tributaries of Arga river, all of them in subcantabrian valleys in Navarre. Originally, the association was meant to include ash forests growing on the banks of small streams where alder was absent, but Biurrun (1999) mentioned that it was also present in rivers with enough water flow to support the growth of alder. In these rivers, *Carici-Fraxinetum* would occupy an external position, between the alder forest and the zonal vegetation, i.e., the mesic oak forest. This alder forest growing on the frequently flooded riverbanks belongs to the association *Lonicero xylostei-Alnetum glutinosae*, first described by Biurrun et al. (1994) (under the name *Hyperico androsaemi-Alnetum glutinosae loniceretosum xylostei*), who provided 18 relevés from subcantabrian valleys, most of them with *Alnus glutinosa* as the dominant species. This association was recognized by Douda et al. (2016) in their pan-European survey of alder forests but was synonymized to *Carici-Fraxinetum excelsioris* in the Iberian survey by Biurrun et al. (2016). Whether there is a place for two riparian forests in subcantabrian rivers remains unresolved, as this work has focused on the upper riverbanks. It is worth highlighting that our clustering analysis has included in this association one plot from Urrobi river, unlike the rest of plots from this river, classified in the western Pyrenean *Galio-Fraxinetum*. This plot is located in the upper section of Urrobi, in the high plateau of Burguete, which is also the eastern limit of *Quercus robur* and mesic oak forests in the region.

The submediterranean association *Viburno lantanae-Ulmetum minoris* was formally described by Biurrun and García-Mijangos (2002b) to include floodplain elm and ash forests from the Castilian-Cantabrian biogeographic sector (Mediterranean region), with 14 relevés from northern Burgos to Eastern Navarre. The type of the association was sampled in Irati river (San Vicente, Lumbier), at a location where we have resurveyed the historic plot for this study. Similarly to the *Carici pendulae-Fraxinetum excelsioris*, this association was provisionally and thus invalidly published by Biurrun (1999), who already indicated that this forest occupies an external position to the alder and willow flooded forests of the association *Humulo-Alnetum* in rivers, while in small streams they grow on the riverbank. Although elm is not usually a dominant species, it can reach high cover beneath the upper canopy formed by ashes, and according to our observations, some big elms can also be found. Elm individuals do not only correspond to *Ulmus minor*, but also to *Ulmus laevis*, which was indicated as a naturalized species in Flora iberica (Navarro and Castroviejo 1993), but recent molecular findings revealed that it originates from the Iberian Peninsula (Fuentes-Utrilla et al. 2014).

The three associations, *Carici-Fraxinetum excelsioris*, *Galio-Fraxinetum excelsioris* and *Viburno-Ulmetum minoris*, were included by Biurrun et al. (2016) in the alliance *Alnion incanae*, but they argued important floristic differences towards Central European floodplain forests to support their proposal of a new suballiance *Buxo semper-virentis-Alnenion glutinosae*. This new suballiance included non-pioneer temperate and submediterranean floodplain

forests from the southern piedmonts of the Pyrenees, Basque-Cantabrian mountains and Cantabrian range (Biurrun et al. 2016), and replaced in northern Spain the two suballiances described from Central Europe: *Alnenion glutinoso-incanae* Oberd. 1953 and *Ulmenion* Oberd. 1953, which include streamside and spring-fed forests, and alluvial hardwood forests in large rivers, respectively (Douda 2008; Petrášová and Jarolímek 2012). However, shortly after the publication of the Iberian review, the European checklist of high level syntaxa was published (Mucina et al. 2016), where the name *Fraxino-Quercion roboris* Passarge 1968 was recovered to include the associations traditionally assigned to *Ulmenion* in the vegetation syntheses of western and central Europe (Wallnöfer et al. 1993; Stortelder et al. 1999), except for some that only indicated the four main hierarchical levels (Chytrý 2013). The French vegetation prodrome also separates both floodplain forest types, but indicates the name *Ulmon minoris* (Oberd. 1953) Seytre et Renaux in Renaux et al. 2019 (basionyme *Ulmenion minoris* Oberd. 1953) for true alluvial hardwood forests, while applied the name *Fraxino-Quercion roboris* for hygrophilous non-alluvial forests (Renaux et al. 2019). Relationships of the northern Iberian suballiance *Buxo-Alnenion glutinosae* with the submediterranean alliance *Alno-Quercion roboris* should also be explored. The latter gathers alder-oak riparian floodplain forests on nutrient-rich alluvial soils in the Apennine and Balkan peninsulas (Mucina et al. 2016; Preislerová et al. 2022), but they are mostly restricted to marshy places (Brullo and Spampinato 1999).

Therefore, the question now arises which is the correct classification at alliance level of the Iberian riparian forests currently classified in the *Buxo-Alnenion glutinosae* and the *Alnion incanae*. Should *Buxo-Alnenion* be transferred to *Fraxino-Quercion roboris*? Or to *Alno-Quercion roboris*? Should it be kept in *Alnion incanae*? According to the ecological conditions, while it is evident that these forests are not growing on the floodplains of big river valleys, it is also true that many stands are not subject to frequent floods but are affected by the fluctuations in the ground water table and irregularly by short-term flooding, as are stands included in *Ulmenion* (Petrášová and Jarolímek 2012), and consequently in *Fraxino-Quercion roboris*. Moreover, the forest structure in *Ulmenion* is also quite similar to our studied forests, with a well-developed and species-rich shrub layer and high cover of the herb layer, with an important temporal turnover between spring and summer. Similar to our forests, low geophytes prevail in spring, while higher hemicryptophytes dominate later (Petrášová and Jarolímek 2012; Pielech 2021).

Species composition also approaches Iberian hardwood forests to *Fraxino-Quercion*, as species typical of mesic forests are common, and the abundance of *Acer campestre* and *Ligustrum vulgare*, among other woody species, separates them from typical *Alnion incanae* stands (Renaux et al. 2019). Using only trees and tall shrubs, Willner (2024) classified Austrian forests at the level of alliance, resulting in a clear separation of *Alnion incanae* and *Fraxino-Quercion*, which led the author to suggest keeping

the hardwood alluvial forests of *Fraxino-Quercion roboris* within the zonal class *Carpino-Fagetea*. Among the diagnostic species of *Fraxino-Quercion* in Austria *Acer campestre* stands out once again, although in this case the ash species bring contrasting arguments, as *Fraxinus excelsior* and *F. angustifolia* appear as diagnostic of *Alnion incanae* and *Fraxino-Quercion*, respectively. However, we must consider that when taken altogether, both ash species are constant in our dataset, and that Austrian hardwood forests are a special Pannonic type where *F. angustifolia* replaces *F. excelsior*, which is typical in many other Central European hardwood riparian forests (Chytrý et al. 2020).

Preislerová et al. (2024) provide only minor differences among both alliances regarding their structural and ecological attributes, such as the presence of broad-leaved evergreen shrubs as dominants in *Alnion incanae*, or the affinity of this alliance for moist to wet substrate, while *Fraxino-Quercion* is limited to intermittently wet substrate. In any case, these attributes are based on the current syntaxonomy, therefore there is an intrinsic circularity on their assignation to the alliances, as is evidenced by the geographical and biogeographical attributes: while *Alnion incanae* is present in the Mediterranean region, *Fraxino-Quercion* is absent; similarly, *Alnion incanae* is indicated from lowlands to the montane belt, while *Fraxino-Quercion* is restricted to lowlands. It is clear that these differences cannot be considered, as they would disappear if *Buxo-Alnenion* was transferred from *Alnion incanae* to *Fraxino-Quercion*.

The correct classification of *Buxo-Alnenion glutinosae* is only a small-scale aspect of the more complex issue of the floristic, ecological and geographical delimitation of the alliance *Alnion incanae* regarding the temperate and submediterranean alluvial forests of the *Fraxino-Quercion roboris* and the *Alno-Quercion roboris*, respectively, as well as their relationship with the mesic oak forests of the order *Carpinetalia betuli*, already brought up by Willner (2024). The pan-European classification of floodplain forests conducted by Douda et al. (2016) did not attempt to distinguish stream and seepage forests from hardwood forests, and included them all in the alliance *Alnion incanae*, without any mention to suballiances. This is understandable as they dealt not only with temperate riparian forests, but also with Mediterranean ones and alder carrs. Therefore, and once the internal classification of European mesic oak forests has been clarified (Novák et al. 2023), we call here for a comprehensive analysis of European temperate riparian, alluvial and mesic oak forests with the aim to clarify the number of alliances and define them with regards to floristic composition, site conditions and biogeography, based on a clear definition of the alliance concept (Willner 2020).

### Diversity patterns along environmental gradients

The three associations show high levels of vascular plant species richness, which is expected due to the relatively high productivity of floodplain habitats, but as predicted

by the hump-shape model of productivity-richness relationship (Grime 1979), the indicator value of soil nitrogen is significantly lower in the most species-rich association, i.e., *Galio-Fraxinetum* (see Figure 9). This is consistent with the results provided by Slezák et al. (2022), who found that species richness declined with productivity in Slovakian floodplain forests. Interestingly, light conditions and soil reaction are highest in *Viburno-Ulmetum*, which shows relatively low species richness, although light and soil pH have emerged as positively influencing species richness in forests (Chiarucci et al. 2001; Wohlgemuth et al. 2008; Hofmeister et al. 2009; Dormann et al. 2020) with open canopy forests with moderately high soil pH being the richest ones. It was not the aim of this study to model the species richness of the studied forests; however, it seems that other factors are more important than light and soil pH for species richness in the context of riparian hardwood forests in northern Iberian Peninsula. If we pay attention to the variables included in the modelling of richness of European deciduous forests in Večeřa et al. (2019), the three top-ranked predictors were temperature seasonality, annual precipitation and forest area. At our regional scale, the richest association *Galio-Fraxinetum* receives the highest annual precipitation (although without significant differences with *Carici-Fraxinetum*), but assuming temperature annual range as a proxy of temperature seasonality, the highest values are in *Viburno-Ulmetum*, which has, together with *Carici-Fraxinetum*, the lowest species richness. In the absence of modeling, we can conclude that alpha richness of these hardwood forests is driven by a set of biogeographic and environmental factors. Among them, the mountainous character of the western Pyrenean *Galio-Fraxinetum*, linked to lower site productivity and higher flooding intensity, might be a positive factor for its high alpha species richness, as already observed in Central European floodplain alder forests, where richness was significantly higher in the Carpathians compared to the Polish Plain and the Pannonic lowland (Hrvínak et al. 2022). This mountainous character is also reflected on the high soil heterogeneity in *Galio-Fraxinetum*, where cover of stones, rocks and gravel is higher than in the other forest types, leading to higher local species richness. Schuster and Diekmann (2005) already stated the importance of micro-heterogeneity in habitat resources, especially edaphic factors, for the determination of species diversity patterns in deciduous forests.

Shannon diversity is lowest in the submediterranean forests of the *Viburno-Ulmetum minoris*, with significant differences regarding the two other forest types. This is especially relevant if we compare it to species richness, as *Viburno-Ulmetum* and *Carici-Fraxinetum* show similar values. This might be due to the fact that submediterranean forests receive more light in the ground layer (see Figure 9), where a few ruderal or grassland species are able to achieve high cover values: *Rubus caesius*, *Urtica dioica*, *Carex flacca*, *Melissa officinalis* and even herbaceous climbers as *Humulus lupulus*.

*Viburno-Ulmetum minoris* has the highest Whittaker's beta diversity, i.e., there is higher species turnover

among plots belonging to this association than among plots belonging to *Galio-Fraxinetum* and especially to *Carici-Fraxinetum*. One of the reasons behind this might be that the river system is more complex in the sections where *Viburno-Ulmetum* develops, and we have sampled a higher variety of geomorphological conditions and landscape configurations. It is important to highlight that in our studied forests the environmental distance seems to play a more important role than geographical distance on beta diversity, as has been already seen for other regions (Vega et al. 2020). In fact, the lowest species turnover was measured in *Carici-Fraxinetum*, which is also the forest type where plots altogether are more geographically distant, but, according to our observations, is the most homogeneous regarding site conditions and landscape configuration.

The mean  $z$  values in the studied forests were highest in *Galio-Fraxinetum* (0.32), while *Carici-Fraxinetum* and *Viburno-Ulmetum* shared a lower value of 0.29. Similar values among 0.26 and 0.30 were found by Chiarucci et al. (2001) in several forest types from Tuscany and Qiao et al. (2012) in Chinese forests across large latitudinal and altitudinal gradients. It has to be taken into account that the mentioned studies included all life-forms in the analysis, while we only included herbaceous species and seedlings and saplings of woody species. For comparison, mean  $z$  values were  $\leq 0.24$  in grassland vegetation both at regional (Filibeck et al. 2019) and Palaearctic scale (Dembicz et al. 2021a, 2021b). Although differences were not significant, the higher  $z$  value in the *Galio-Fraxinetum* is probably a consequence of the higher cover of stones, rocks and gravel in this association, as already demonstrated for grassland habitats at regional (Filibeck et al. 2019) and Palaearctic scale (Dembicz et al. 2021a).

### Structural and climatic variables

The most relevant structural differences among forest types refer to the cryptogam cover, i.e., the moss cover, and the cover of stones, rocks and gravel. These parameters are significantly higher in the *Galio-Fraxinetum*, probably related to the more torrential water flow, which allows the deposition of coarse material and the removal of accumulated litter and thus offering more space for bryophyte development.

The submediterranean forests of *Viburno-Ulmetum* showed significant climatic differences regarding the two *Fraxinus excelsior*-dominated associations. It is worth highlighting the low value of the summer ombrothermic index ( $Ios_3$ ), close to the threshold that defines the Mediterranean climate. This result is in line with the results of Biurrun et al. (2014), who analyzed riparian forests of northern Iberian Peninsula and found that the threshold value of the ombrothermic index of the two warmest months ( $Ios_2$ ) for a true Mediterranean climate, i.e.,  $Ios_2 < 2$  approximately coincides with the replacement of *Fraxinus excelsior* by *F. angustifolia*.

## Conclusions

The present study represents the first attempt to assess the relationships between species richness and spatial scale in Iberian forest ecosystems. With this aim we have adapted to forest habitats the EDGG sampling protocol developed for the nested sampling of grasslands and other open habitats. Moreover, we have established such nested plots as permanent plots that will facilitate monitoring the effects of global change on these forests. This is particularly relevant because hardwood riparian forests are especially vulnerable to climate change in northern Iberian Peninsula, as this region represents their European southwestern distribution limit. Their fragility facing climate change and their high conservation value, both as an endangered and diverse habitat and as refuge for threatened flora and fauna commit us to in-depth investigate their diversity patterns and ecological requirements. It becomes evident that in order to establish efficient conservation measures we need to clarify their identity both in the frame of EUNIS habitat classification and the European phytosociological classification system.

## Data availability

Full plot-level information, including geographic coordinates and composition data, are available under request from the Vegetation Database of the University of the Basque Country (EU-00-011), as well as from JB and IS, who also store the data of the nested-plot series.

## Author contributions

IB and JAC planned the research, JB and IS conducted the field sampling with participation of IB and JAC, IB performed the vegetation classification and diagnostic species analyses and led the writing, IS and JAC calculated the diversity indices and performed the ANOVAs and permutation tests, JB prepared the map, extracted the climatic variables and performed the EUNIS-Esy and the ordination analysis, and all authors critically revised the manuscript.

## Acknowledgments

We would like to express our gratitude to Itziar García-Mijangos, who helped with the expert system, and to Eneko Barriola and Denys Vynokurov, who helped with the sampling. This work has been funded by the Basque Government (IT1487-22), Jokin Belmonte has been supported by Next Generation funds from the European Union (Investigo Program n°58) and Irati Sanz-Zubizarreta by a predoctoral grant of the University of the Basque Country UPV/EHU (PIF21/255).

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## Supplementary material

### Supplementary material 1

#### Header data and metadata of the 72 plots (\*.xlsx)

Link: <https://doi.org/10.3897/VCS.145406.suppl1>

### Supplementary material 2

#### Full synoptic table with relative frequency values of all species across the three forest types (\*.xlsx)

Link: <https://doi.org/10.3897/VCS.145406.suppl2>